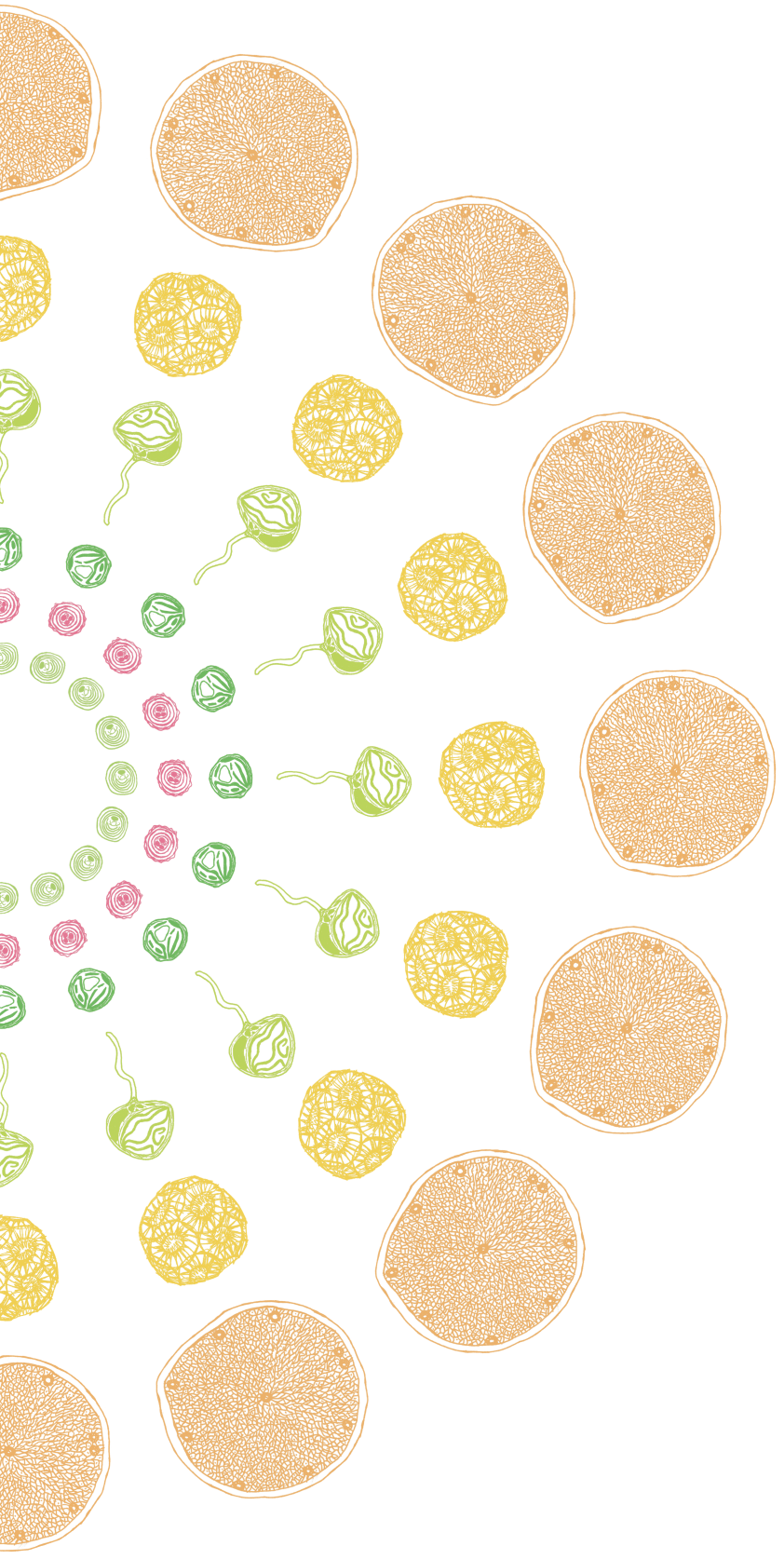

Chapter 7

Summary

Introduction

The open oceans play a key role in biogeochemical processes on Earth. By means of photosynthesis, phytoplankton communities in oligotrophic and mesotrophic oceanic regions are responsible for up to 40% of the total global net primary production (Field *et al.* 1998). This does not only provide the basis for the marine food web, but also has a strong impact on carbon sequestering in the ocean's interior (Falkowski *et al.* 1998). The understanding of phytoplankton performance in open ocean ecosystems is often limited by the complexity of the changes in temperature, nutrient, and irradiance conditions throughout the water column. In addition, little information was available on the (photo)physiological response of specific oceanic phytoplankton species to these water column conditions. Large environmental studies have related water column conditions to the distribution of phytoplankton throughout the open oceans (Agawin *et al.* 2000, Li *et al.* 2002, Johnson *et al.* 2006). For example, the spatial and temporal patterns in the overall size structure of phytoplankton communities have been explained by variation in temperature, with picophytoplankton dominating in warm tropical waters (Agawin *et al.* 2000, Feng *et al.* 2009, Morán *et al.* 2010). Moreover, recent observations showed a shift in community structure over a variety of taxonomic levels. Prokaryotic picophytoplankton species dominate the phytoplankton community during strong thermal stratification and eukaryotic picophytoplankton dominate during increased mixing in the surface layers of the open oceans (Bouman *et al.* 2011). The present study showed the physiological basis for the differential distribution of prokaryotic and eukaryotic oceanic phytoplankton and their contribution to primary production in the open oceans (Chapter 2, 3, 4, 5, 6). The following questions were addressed in this thesis:

1. What are the (interactive) effects of irradiance, temperature, and nutrient availability on the photophysiology of different oceanic phytoplankton species?
2. How does variation in photophysiology of different prokaryotic and eukaryotic oceanic phytoplankton species affect the sensitivity to excessive PAR and UVR?
3. How does genotypic and phenotypic variation in photophysiology affect photosynthetic and growth rates in prokaryotic and eukaryotic oceanic phytoplankton species?

Photophysiology of oceanic phytoplankton

In the present study, distinct differences in photophysiology between prokaryotic and eukaryotic oceanic phytoplankton species were observed (Chapter 2, 3, 4, 5). This was related to genotypic variation in light harvesting and photoprotective pigmentation, chlorophyll *a* specific absorption, and photoregulating mechanisms (Chapter 2, 3, 4, 5). For example, the initial response to varying irradiance conditions could be significantly faster in eukaryotic phytoplankton species compared with prokaryotic phytoplankton species due to the presence of a photoprotective (xanthophyll) pigment cycle (Chapter 2). The (phenotypic) variation in photophysiology of different prokaryotic and eukaryotic oceanic phytoplankton species was further studied under varying irradiance (Chapter 2), temperature (Chapter 3), and nutrient (Chapter 5) conditions.

Irradiance

The photophysiological response to varying irradiance conditions was different between prokaryotic and eukaryotic oceanic phytoplankton species (Chapter 2). In the prokaryotic phytoplankton species *Prochlorococcus marinus* (high light adapted ecotype) and *Synechococcus* sp. (low and high light adapted ecotypes), no changes in cellular chlorophyll *a* were observed during photoacclimation to varying irradiance conditions (10-125 µmol photons m^{-2} s^{-1}), whereas photoprotective pigmentation increased during photoacclimation to higher irradiance intensities (Chapter 2). In *P. marinus*, changes in pigmentation also included a reduction in chlorophyll *b*/*a* at high irradiance intensities (Chapter 2), whereas in *Synechococcus* sp., changes in the main light harvesting pigments of the phycobilisome might have been involved (Kana & Glibert 1987, Palenik 2001). In addition, chlorophyll *a* specific absorption increased considerably in *P. marinus* during photoacclimation to high irradiance intensities (Chapter 2). Although *P. marinus* and *Synechococcus* sp. were able to alter their photophysiology in response to varying irradiance intensities, the photoacclimation potential was lower compared with eukaryotic phytoplankton species. This was especially evident from the reduced growth rates at high irradiance intensities (Chapter 2). In the eukaryotic phytoplankton species *Ostreococcus* sp., *Emiliania huxleyi*, and *Thalassiosira oceanica*, a relatively uniform response to irradiance was observed that was comparable to earlier observations in eukaryotic phytoplankton (Chapter 2, Falkowski & La Roche 1991, Johnsen & Sakshaug 1996, MacIntyre *et al.* 2000). Cellular chlorophyll *a* concentrations decreased during photoacclimation to high irradiance intensities, whereas chlorophyll *a* specific absorption remained unchanged. In addition, the relative amount of the xanthophyll cycle pigments increased at higher irradiance intensities. The high photoacclimation potential of the eukaryotic oceanic phytoplankton species resulted in enhanced production and growth rates at high irradiance intensities (Chapter 2).

Temperature

The photophysiology of oceanic picophytoplankton was further assessed by the response to varying temperature conditions (Chapter 3). Typically, phytoplankton acclimated to low temperatures show a photophysiology comparable to that of high light acclimated phytoplankton, with low levels of cellular chlorophyll *a* (Geider 1987, Maxwell *et al.* 1994, Stramski *et al.* 2002). In the present study, this was also observed in the oceanic picophytoplankton species *P. marinus*, *Prochlorococcus* sp. (low light adapted ecotype), *Ostreococcus* sp., and *Pelagomonas calceolata* between 16 ºC and 24 ºC (Chapter 3). In response to elevated temperatures, these oceanic picophytoplankton species extended their light harvesting capacity by an increase in cellular chlorophyll *a* concentrations (Chapter 3). In *P. marinus*, *Prochlorococcus* sp., and *Ostreococcus* sp., this was accompanied by a decrease in photoprotective pigmentation. Although the changes in the light harvesting complex are typically associated with a decrease in light absorption due to changes in pigment packaging (Geider 1987, Stramski *et al.* 2002, Hancke *et al.* 2008), this was not observed in *P. marinus*, *Prochlorococcus* sp., *Ostreococcus* sp., and *P. calceolata*. It is possible that the changes in light absorption are restricted by the relatively small effect of pigment packaging in picophytoplankton compared with larger phytoplankton species (Bricaud *et al.* 1999). In addition to changes in the light harvesting complex, electron transport rates also increased during acclimation to elevated temperatures in *P. marinus*, *Prochlorococcus* sp., *Ostreococcus* sp., and *P. calceolata*. Further analysis of the electron transport characteristics showed enhanced photoacclimation to higher irradiance intensities at elevated temperatures for the oceanic picophytoplankton species. This was also evident from the increase in the maximum quantum yield of photosystem II (F_v/F_m). The enhanced photoacclimation was accompanied by reduced photoinhibition in *P. marinus*, *Ostreococcus* sp. and *P. calceolata*, suggesting that oceanic picophytoplankton are less susceptible to the negative effects of high irradiance intensities at higher temperatures.

Nutrients

Finally, the photophysiological response to nutrient availability was assessed in oceanic phytoplankton (Chapter 5). Although species specific differences were observed in the photophysiological response to low nutrient availability, the response uniformly resulted in lower transfer efficiencies of light harvesting energy and reduced growth during N and P starvation in *P. marinus*, *Ostreococcus* sp., and *T. oceanica*. In the prokaryotic phytoplankton species *P. marinus*, the light harvesting capacity was increased at low nutrient availability. Cellular chlorophyll *a* concentrations did not vary during nutrient starvation, whereas chlorophyll *a* specific absorption increased considerably. However, the increase in light harvesting capacity at low nutrient availability was accompanied by decreased functioning

of photosystem II (PSII), thereby reducing the transfer of light energy (Chapter 5, Steglich *et al.* 2001, Lindell *et al.* 2002). In the eukaryotic phytoplankton species *Ostreococcus* sp., changes in cellular chlorophyll *a* coincided with those in chlorophyll *a* specific absorption, suggesting that the light harvesting capacity was not affected by nutrient availability (Chapter 5). The eukaryotic phytoplankton species *T. oceanica* showed a similar response during P starvation. However, cellular chlorophyll *a* concentrations decreased during N starvation in *T. oceanica*, which was accompanied by alterations in pigment packaging and the consequent increase in chlorophyll *a* specific absorption. This response is comparable to that observed in other nanophytoplankton species at low nutrient availability (Geider *et al.* 1993, Berges & Falkowski 1998, Loebl *et al.* 2010). In both *Ostreococococcus* sp. and *T. oceanica*, changes in the light harvesting capacity included an increase in photoprotective pigments and enhanced thermal dissipation of excess energy by the xanthophyll pigment cycle (Chapter 5). This resulted in reduced transfer of light harvesting energy through PSII.

Excess irradiance sensitivity of oceanic phytoplankton

The present study showed that during short periods of high irradiance exposure (500 µmol photons m^{-2} s^{-1}), both prokaryotic and eukaryotic oceanic phytoplankton were susceptible to photoinhibition (Chapter 4, 5). Moreover, prolonged periods of high irradiance exposure may lead to significant viability loss in oceanic phytoplankton (Chapter 5). The response to high irradiance was species specific and appeared to be related to the genetically defined light adaptation of the different species. This was not only evident from differences between ecotypes of *Prochlorococcus* spp., but also from differences between eukaryotic phytoplankton species. The low light adapted ecotype *Prochlorococcus* sp. and the eukaryotic species *P. calceolata* were highly sensitive to high photosynthetically active radiation (PAR, 400-700 nm), whereas the high light adapted ecotype *P. marinus* and the eukaryotic species *Ostreococcus* sp. and *T. oceanica* showed lower sensitivity (Chapter 4, 5). Additional exposure to ultraviolet radiation (UVR, 280-400 nm) led to higher photoinhibition in oceanic phytoplankton, except in the eukaryotic phytoplankton species *Ostreococcus* sp. (Chapter 4). Overall, the diatom species *T. oceanica* showed lowest photoinhibition and viability loss during high irradiance exposure (Chapter 5).

Photoregulating mechanisms

The variation in high light sensitivity between specific phytoplankton species was related to the presence and efficiency of photoregulating mechanisms. In all phytoplankton species, photoregulation occurred by the dissipation of excess energy through non photochemical quenching. In *P. marinus* and *Prochlorococcus* sp., the underlying mechanisms of fast

relaxing non photochemical quenching remained unknown, but the present study showed that this process was influenced by temperature and UVR (Chapter 4). This suggests that fluidity and stability of the thylakoid membrane played an important role in the dissipation of excess energy in *P. marinus* and *Prochlorococcus* sp. (Chapter 4). In addition, the presence of the xanthophyll pigment zeaxanthin and the decoupling of light harvesting antennas from PSII may have offered photoprotection in *P. marinus* (Chapter 2, 5), but this was not related to non photochemical quenching (Chapter 4, 5). In the eukaryotic phytoplankton species *Ostreococcus* sp., *P. calceolata*, and *T. oceanica*, fast relaxing non photochemical quenching coincided with the de-epoxidation of the xanthophyll pigment cycle (Chapter 4, 5). This offered substantial photoprotection in *Ostreococcus* sp. and *T. oceanica*, but to a lesser extend in *P. calceaolata*. In addition to the regulation of light harvesting energy by the xanthophyll pigment cycle, alternative electron transport mediated by a propyl gallate-sensitive oxidase (PTOX) played an important role in *Ostreococcus* sp. (Chapter 5, Cardol *et al.* 2008). This process does not only offer photoprotection by deviating electrons away from the photosystems, but may also promote the de-epoxidation of the xanthophyll pigment cycle by an increase in the trans-membrane proton gradient (Chapter 4, 5, Cardol *et al.* 2008, Goss & Jakob 2010). Although PTOX mediated alternative electron transport supported survival during high irradiance exposure in *T. oceanica*, it is unclear whether this mechanism functions in a similar fashion as compared with *Ostreococcus* sp. (Chapter 5, Cardol *et al.* 2008). In contrast to earlier suggestions (Mackey *et al.* 2009, Berg *et al.* 2011), evidence for photoregulation by PTOX mediated electron transport was not found in a high light adapted ecotype of *Prochlorococcus* spp. (eMED4) (Chapter 5).

Phenotypic variation in photoregulation

The high light sensitivity of specific phytoplankton species was further influenced by alterations in photophysiology induced by varying irradiance, temperature, and nutrient conditions. The present study showed that photoacclimation to high irradiance intensities decreased light harvesting pigmentation and increased photoprotective pigmentation in oceanic phytoplankton (Chapter 2). In addition, the de-epoxidation of the xanthophyll pigment cycle increased during high light acclimation in the eukaryotic species *Ostreococcus* sp., *E. huxleyi*, and *T. oceanica* (Chapter 2). Although the response to excess irradiance intensities after photoacclimation to varying irradiance conditions was not directly measured in the present study, earlier observations in other phytoplankton species suggest that the observed changes in pigmentation would reduce the sensitivity to excess irradiance intensities (Van de Poll *et al.* 2005, Van de Poll *et al.* 2006, Dimier *et al.* 2007b). This was partly confirmed by the reduced photoinhibition of carbon fixation after high light acclimation in the eukaryotic phytoplankton species *Ostreococcus* sp., *E. huxleyi*, and *T. oceanica* (Chapter 2).

Temperature acclimation also influenced photoinhibition and related processes during high irradiance exposure in oceanic phytoplankton. Not only were species acclimated to higher irradiance intensities at elevated temperatures (Chapter 3), but temperature acclimation also influenced the response to high irradiance exposure by changes in the relative contribution of photoinhibition and photoprotective mechanisms to non photochemical quenching (Chapter 4). In the prokaryotic species *P. marinus* and *Prochlorococcus* sp., improved fluidity of the thylakoid membrane and/or enzymatic reactions likely enhanced photoprotection at elevated temperatures (Chapter 4). In the eukaryotic phytoplankton species *Ostreococcus* sp., the de-epoxidation of the xanthophyll pigment cycle and possibly alternative electron transport were enhanced at elevated temperatures, whereas in *P. calceolata*, photoinhibition was reduced (Chapter 4). In addition, elevated temperatures had a beneficial effect on the response to high irradiance intensities by partially counteracting the UVR-induced photoinhibition in *P. marinus*, *Ostreococcus* sp., and *P. calceolata*.

Nutrient availability may also have a positive feedback on the high irradiance response of oceanic phytoplankton. *P. marinus*, *Ostreococcus* sp., and *T. oceanica* showed reduced sensitivity to high irradiance exposure when nutrient availability was low, although species specific differences were observed (Chapter 5). In *P. marinus*, the lower sensitivity to high irradiance intensities at low nutrient availability was related to changes in a photoregulating process prior to electron transport that did not involve changes in pigmentation, possibly the decoupling of antenna complexes from PSII. In *Ostreococcus* sp., the reduced high irradiance sensitivity was related to enhanced photoprotection by the xanthophyll pigment cycle or alternative electron transport, depending on the limiting nutrient. In *T. oceanica*, enhanced photoprotection by the xanthophyll pigment cycle ensured lower sensitivity to high irradiance exposure when nutrient availability was low.

Photosynthetic and growth rates of oceanic phytoplankton

The variation in photophysiology and photoregulation may lead to considerable differences in photosynthetic and growth rates in oceanic phytoplankton species. Although phenotypic variation in growth rates of specific phytoplankton species were observed under different irradiance and temperature conditions, eukaryotic oceanic phytoplankton showed higher growth rates (0.28-1.40 d^{-1}) compared with prokaryotic oceanic phytoplankton (0.15-0.63 d^{-1}) (Chapter 2, 3, 5). A similar difference between prokaryotic and eukaryotic oceanic phytoplankton was observed in the maximum photosynthetic rate (1.79-8.71 versus 5.88-30.7 µg C µg Chl-a^{-1} h^{-1}) (Chapter 2). The ability to effectively regulate and acclimate to varying irradiance conditions resulted in optimal carbon fixation and growth rates at higher irradiance intensities in the eukaryotic phytoplankton species *Ostreococcus* sp., *E. huxleyi*,

and *T. oceanica* compared with the prokaryotic phytoplankton species *Prochlorococcus* spp. and *Synechococcus* spp. (Chapter 2, 4, 5). Moreover, when *Ostreococcus* sp., *E. huxleyi*, and *T. oceanica* were acclimated to higher irradiance intensities (125 µmol photons m^{-2} s^{-1}), growth was higher during dynamic irradiance conditions, suggesting that eukaryotic phytoplankton species benefit from occasional high irradiance intensities (Chapter 2, 6).

In addition to irradiance induced variation in photosynthetic and growth rates, temperature-dependent differences in the maximal electron transport and growth rates were observed among prokaryotic and eukaryotic oceanic picophytoplankton (Chapter 3). The growth rate of oceanic picophytoplankton species increased at elevated temperatures, but different optimal temperatures for growth were observed between specific phytoplankton strains. Low and high light adapted ecotypes of *Prochlorococcus* spp. and the eukaryotic picophytoplankton species *P. calceolata* showed highest growth rates at 24 °C, whereas the eukaryotic picophytoplankton species *Ostreococcus* sp. showed highest growth rates between 20 and 24 °C (Chapter 3). The overall photophysiology of the two ecotypes of *Prochlorococcus* spp. and the eukaryotic picophytoplankton species moved towards the use of higher irradiance intensities to support the enhanced growth rates at elevated temperatures. This was evident from enhanced light harvesting capacity and electron transport rates and reduced photoinhibition at higher temperatures (Chapter 3, 4). These changes in photophysiology illustrate the interactive effects of temperature and irradiance on photosynthetic and growth rates in oceanic phytoplankton (Chapter 2, 3). An increase in temperature may therefore lead to a broader depth distribution of specific phytoplankton species, but photophysiology and consequent photosynthetic and growth rates remain highly influenced by the specific photoadaptation of different phytoplankton ecotypes and/or species.

Ecological consequences of stratification and vertical mixing

In (permanently) stratified regions of the open oceans, sea surface temperatures are relatively high and thermal stratification strongly reduces the nutrient availability in the euphotic zone. Simultaneously, phytoplankton may experience high (dynamic) irradiance conditions in the upper mixed layer or more stable, low irradiance conditions in the deep chlorophyll maximum. The phytoplankton community of such regions is typically dominated by the prokaryotic phytoplankton genera *Prochlorococcus* spp. and *Synechococcus* spp. and eukaryotic pico- and nanophytoplankton species (Chapter 6, Olson *et al.* 1990, Li 1994, Durand *et al.* 2001). The present study showed that prokaryotic phytoplankton species, such as *Prochlorococcus* spp., may benefit from high temperatures, because these phytoplankton species have a relatively high optimal growth temperature (Chapter 3, 4, 6). Moreover, *Prochlorococcus* spp. and *Synechococcus* spp. may have a competitive advantage over larger (eukaryotic)

phytoplankton species in oligotrophic regions, because their extremely small cell size and consequent large surface area to volume ratio leads to a relative high nutrient affinity and low nutrient demand (Raven 1986, Chisholm 1992, Bertilsson *et al.* 2003, also see elemental composition in Chapter 2, 6). However, the high (dynamic) irradiance conditions in the upper mixed layer may strongly reduce growth in prokaryotic phytoplankton species during stratification (Chapter 2, 4, 5). In contrast, the ability to photoacclimate to a wide variety of both stable and dynamic irradiance conditions may offer eukaryotic pico- and nanophytoplankton species a competitive advantage during stratification and (deep) vertical mixing (Chapter 2). Moreover, the efficient photoregulating mechanisms of eukaryotic phytoplankton leads to a relative lower photoinhibition and viability loss in PAR and UVR rich waters near the surface of open oceans (Chapter 4, 5). These species specific differences in the response to varying irradiance conditions remained evident when the interactive effects of temperature, nutrient availability, and irradiance conditions were considered (Chapter 4, 5). It therefore seems that nutrient availability controls the contribution of eukaryotic phytoplankton to the phytoplankton community during stratification, whereas the contribution of prokaryotic phytoplankton species may be limited by the negative effects of high (dynamic) irradiance conditions near the surface of open oceans.

The distribution of specific phytoplankton species and the consequent community structure may have considerable consequences for primary production and the export of carbon to the ocean's interior. The present study showed that prokaryotic species, such as *Prochlorococcus* spp. and *Synechococcus* spp., show lower photosynthetic and growth rates compared with other oceanic phytoplankton species at comparable environmental conditions (Chapter 2, 3, 5). The dominance of these prokaryotic phytoplankton species in open oceans may therefore directly lead to lower primary production of the phytoplankton community, regardless of nutrient or light limitation (Chapter 6). The primary production of *Prochlorococcus* spp. near the surface may be further reduced by high levels of photoinhibition and significant viability loss during high light exposure (Chapter 4, 5). Moreover, the export of carbon may be relatively low in phytoplankton communities dominated by prokaryotic picophytoplankton, because carbon and nutrients are efficiently remineralized by the microbial loop (Azam *et al.* 1983, Ducklow 1999, Finkel *et al.* 2010). In contrast, the presence of larger nano- and microphytoplankton species can potentially lead to high primary production (Chapter 2, 3, 5) and increased export of carbon by rapid sedimentation of particulate matter (Azam *et al.* 1983, Ducklow 1999, Finkel *et al.* 2010). However, the primary production of eukaryotic phytoplankton may be limited by low nutrient availability in large areas of the open oceans (Chapter 6, Graziano *et al.* 1996, Cavender-Bares *et al*. 2001, Moore *et al.* 2008).

Consequences of global climate change

It is expected that climate change will mediate a rise in seawater temperature by 1.5-4.5 °C over the next century (Houghton *et al.* 1995). The present study showed that this rise in seawater temperature may lead to an increase in photosynthetic and growth rates in oceanic picophytoplankton species (Chapter 3, 4). However, the genetically defined temperature tolerance as well as the optimal temperature for growth determines the actual success of specific phytoplankton species in response to elevated temperatures (Johnson *et al.* 2006, Thomas *et al.* 2012). Specific phytoplankton species, such as the eukaryotic species *Ostreococcus* sp., may not be able to acclimate to elevated temperatures associated with climate change, because their optimal temperature for growth is close to current sea surface temperatures (Chapter 3). This seems to be a general trend in oceanic phytoplankton species from subtropical and tropical regions (Thomas *et al.* 2012). Because growth decreases abruptly above the optimal growth temperature, these phytoplankton species are especially sensitive to an increase in temperature associated with climate change (Chapter 3, Eppley 1972, Thomas *et al.* 2012). However, other oceanic phytoplankton species, such as *Prochlorococcus* spp. and *Pelagomonas calceolata*, showed higher temperature tolerances and may be expected to show increased growth under future temperature conditions (Chapter 3, Johnson *et al.* 2006, Zinser *et al.* 2007). Thus, a rise in sea surface temperature associated with global climate change may directly lead to changes in the species composition of the phytoplankton community in open oceans (also see Beardall & Raven 2004, Finkel *et al.* 2010).

Indirectly, the rise in sea surface temperature may also lead to changes in the structure of phytoplankton communities. The increased thermal stratification associated with climate change will alter nutrient availability and the intensity, spectral composition, and dynamics of phytoplankton irradiance exposure in the surface layers of the open oceans (Boyd & Doney 2002, Behrenfeld *et al.* 2006, Polovina *et al.* 2008). It is expected that the reduced nutrient availability in the surface layers of the open oceans will increase the proportion of picophytoplankton species in the phytoplankton community (Chapter 6, Agawin *et al.* 2000, Morán *et al.* 2010). Prokaryotic picophytoplankton, such as *Prochlorococcus* spp., would especially benefit from this low nutrient availability, because these species have a higher nutrient affinity and lower nutrient demand compared with eukaryotic phytoplankton species (Chisholm 1992, Van Mooy *et al.* 2009, Finkel *et al.* 2010). In contrast, the increased irradiance intensities associated with the shallowing of the upper mixed layer are likely to lead to a competitive advantage of eukaryotic phytoplankton species, such as *Ostreococcus* sp., *E. huxleyi*, and *T. oceanica*, which are less susceptible to high (dynamic) irradiance intensities (Chapter 2, 4, 5). More sensitive species, such as the prokaryotic species *Prochlorococcus* spp., are likely to experience higher photoinhibition and viability loss during these increased

PAR and UVR conditions (Chapter 2, 4, 5). The consequences of climate change on the composition of the phytoplankton community in open oceans are further influenced by the interactive effects of varying temperature, nutrient, and irradiance conditions on phytoplankton performance. For example, the negative effects of high irradiance exposure may be reduced at elevated temperatures and/or low nutrient availability (Chapter 4, 5).

Climate change induced variations in the phytoplankton community may have considerable consequences for the marine food web and the transport of carbon to the ocean's interior. In the North Atlantic Ocean, it was observed that a shift in phytoplankton community composition may lead to variation in phytoplankton biomass and primary production in the surface layers of the stratified oceans (Chapter 6, Gregg *et al.* 2003). This may lead to 25% lower phytoplankton biomass and 22% lower primary production when sea surface temperatures rise by 1 °C (within the temperature range of 12-23 °C, Chapter 6, Gregg *et al.* 2003). Although primary production may also increase as a consequence of climate change on regional scales, overall primary production is expected to decrease in large areas of the open oceans (Bopp *et al.* 2001, Gregg *et al.* 2003, Behrenfeld *et al.* 2006, Lozier *et al.* 2011). Moreover, the shift to smaller phytoplankton species associated with enhanced stratification is likely to increase carbon cycling by the microbial loop (Azam *et al.* 1983, Laws *et al.* 2000, Finkel *et al.* 2010). Carbon sequestering will therefore not only be reduced by lower primary production in the open oligotrophic oceans, but the transport of carbon to the ocean's interior by processes such as sedimentation is also likely to decrease during climate change.